

Notes on *Ceramium* (Rhodophyta: Ceramiales) from the Hawaiian Islands¹

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ABSTRACT: *Ceramium* is widely distributed and recorded from the coasts of the North Pacific Ocean. Thus, it is not surprising to find new species and new records of this genus among the numerous islands spread in this oceanic region. Extensive examination of material collected around O'ahu and other Hawaiian Islands has yielded two new records: *Ceramium aduncum* Nakamura (previously known from Japan), *Ceramium clarionensis* Setchell & Gardner (previously recorded for the Pacific coast of Mexico), and a new species, *Ceramium cingulum* Meneses.

APPROXIMATELY 55 SPECIES of the genus *Ceramium* (Ceramiales) have been reported for the tropical and subtropical North Pacific Ocean, representing about one-half of the known species worldwide. Detailed descriptions as well as passing references in marine floras of this region describe species mainly from the Pacific coast of North and Central America (Setchell and Gardner 1924, 1930, 1937, Dawson 1944, 1945a,b, 1954a,b,c, 1957b, 1961, 1962, Hollenberg 1948) and Japan (Yendo 1917, Nakamura 1950, 1965, Itono 1972, 1977).

In Hawai'i, records of *Ceramium* species have been made since about 1876 (Abbott 1980), and a number have been published (Abbott 1947, 1980, Hollenberg 1968, Doty et al. 1974, Norris and Abbott 1992).

Recognition and interpretation of seasonal and environmental modifications of the thallus (Dixon 1960, Garbary et al. 1978, Womersley 1978, Suh and Lee 1984) have contributed to a clarification of the taxonomic standing of some species in *Ceramium*. Thus, some of the originally described species have been reduced to synonymy, and the species delimitation in the genus is undergoing a series of changes resulting from critical examination of the diagnostic features.

Species of *Ceramium* are common around

the island of O'ahu, Hawai'i, appearing in almost any collection made, mainly as epiphytes. Recently, four new species were recorded (Norris and Abbott 1992). The goal of the study reported here was to include all possible morphological variations in the *Ceramium* taxa collected. Thus, intensive collections were made around O'ahu, and collections from other Hawaiian Islands were examined. As a result three new records and one new species of *Ceramium* are reported.

MATERIALS AND METHODS

Haphazardly sampled collections were made at several sites around the island of O'ahu. Localities were chosen on the basis of habitat diversity and accessibility.

Specimens were preserved in 2–5% buffered formalin/seawater and dried and pressed on herbarium sheets or fixed and preserved as whole mounts on permanent microscope slides. Material preserved on slides was stained with 1% aqueous solution of aniline blue slightly acidified with hydrochloric acid (Tsuda and Abbott 1985). Plants were mounted in 25% solution of clear Karo corn syrup (Best Foods, CPC International, Englewood Cliffs, New Jersey) in distilled water with a few crystals of phenol added as a preservative. This procedure stained axial cells differentially from cortical cells in *Ceramium*, while highlighting the primary pit connections. Observations and measurements were made using a light microscope (Zeiss).

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Nodal and internodal measurements, cell sizes, number of cortical cell rows, and other data are given in ranges in which the numbers in parentheses indicate the extreme values of the entire range and the other numbers are the extremes that include 75% of the individuals recorded.

Herbarium specimens examined include material from the National Museum of Natural History, Smithsonian Institution (US), Isabella A. Abbott personal collection (IAA), the Herbarium of the University of California at Berkeley (CAS in UC), and my personal collection (TM). A set of microscope slides bearing my Hawaiian study material has been deposited in the Herbarium of the Bernice P. Bishop Museum (BISH), with some duplicates at the Universidad Católica de Chile (SSUC).

Ceramium aduncum Nakamura

Figures 1–4

Ceramium aduncum Nakamura, 1950:158–160, figs. 2b, 3; 1965:119–180, pl. II, figs. 1–2; Itono, 1972:81, fig. 11a. Synonyms: *C. circinatum* Yendo (non Agardh), 1917:92–93. *Ceramium* “sp. nov.” Setchell & Gardner, 1930:173, pl. 7, fig. 25. *C. clarionensis* sensu Dawson (non Setchell and Gardner), 1950:134, pl. 4, fig. 29; 1954b:448, fig. 55K; 1956:54; 1961:440; 1962:53, pl. 18, figs. 5–6.

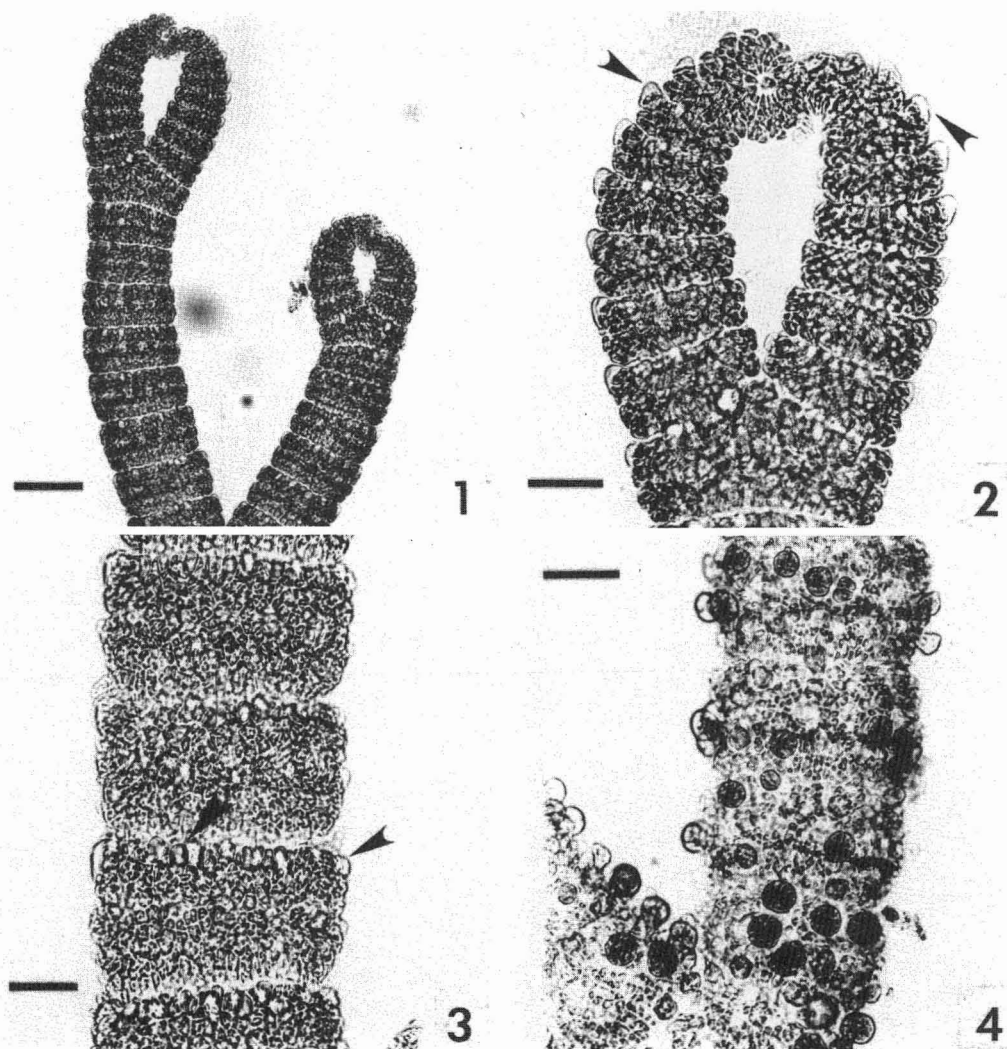
Plants epiphytic on species of *Galaxaura*, *Acanthophora*, and *Gracilaria* or entangled with other algae, forming small turfs on protected shallow subtidal reef flats. Thallus 4–15 mm tall, basal portions creeping on the substrate. Branching pattern dichotomous, mature plants with up to six dichotomies; adventitious branches infrequent. Apices strongly forcipate with outer margins dentate (Figures 1, 2). Attachment by means of two types of rhizoids, two to three cells long ending in a blunt apex, or one-celled ending in a discoid base with small digitations, both types 16–22 μm (occasionally 30 μm) thick. Internodes nearly up to 1.5 times as long as wide; 160–240 μm in diameter, 94–176 μm (sometimes up to 290 μm) long in the lower creeping portions of the plant and 144–240 μm in diameter, 12–108 μm (seldom 240 μm) long in the upright portions. Nodes slightly

protruding, consisting of a central row of large cells with three to six layers of smaller outer cells irregularly arranged; nodal diameter 1.9 times the diameter of the internodes (Figure 3); 170–280 μm in diameter, 64–170 μm long in basal portions of the plant; 140–240 μm (up to 280 μm) in diameter, 48–150 μm long in upright portions. Cortical cells 13–19(25) μm long by 6–9 μm wide; roundish to somewhat angular in shape except for those located in the lowest nodal row, where they are axially elongated. Gland cells (15)19–31 μm by 11–20 μm , abundant or scarce, scattered throughout the nodes (Figure 3), especially in the younger parts of the plant. Tetrasporangia (Figure 4) borne on cortical cells, initially adaxial and later surrounding the entire node, rounded, thick-walled, 38–51 by 35–54 μm , involucre absent. Gametangial plants were not observed.

REMARKS: *Ceramium aduncum* was described by Nakamura (1950:158–160) and reported from Taiwan to Hokkaido. Nakamura (1950: figs. 3a and f) illustrated tetrasporangial plants in which the cortical bands are somewhat reduced when compared with the Hawaiian plants, whereas the broader nodes depicted for a cystocarpic plant seem more in agreement with the nonreproductive material from O‘ahu.

Nakamura (1950:159–160) mentioned the similarity of his material to a possible new species of *Ceramium* reported by Setchell and Gardner (1930) from sterile material from Guadalupe Island. Because of the scanty material available and its lack of reproductive organs, no name was proposed for the species. Examination of this material (UC 1462250/Mason 169) showed that it consists of one dichotomous branch with typical well-developed *C. aduncum* nodes and abundant gland cells characteristic of this species. There is no doubt that the *Ceramium* “sp. nov.” of Setchell and Gardner (1930) is the same species as *C. aduncum* Nakamura.

In the same publication, Setchell & Gardner (1930:170–171) described *Ceramium clarionensis* from Clarion Island (Revillagigedo Islands, Pacific coast of Mexico) as a species with distinctive protruding involucre



FIGURES 1–4. *Ceramium aduncum* Nakamura. 1, Forcipate apices; scale = 140 μ m. 2, Close-up showing gland cells (arrowheads); scale = 55 μ m. 3, Close-up of lower portion of thalal showing compact nodal structure and gland cells located in the upper portion of the nodes; scale = 50 μ m. 4, Tetrasporangial plant; scale = 85 μ m.

tetrasporangia, 65–75 μ m diameter, borne on the abaxial side of the filaments. Dawson (1950:134–137) later reported *C. clarionensis* from the Gulf of California and along the Pacific coast of southern California and northern Mexico. However, Dawson's description and figures (1950:pl. 4, fig. 29) agree with descriptions of *C. aduncum* by Nakamura (1950) and the *Ceramium* sp. nov.? of Setchell and Gardner (1930) and

not with *C. clarionensis*. Examination of material identified by Dawson as *C. clarionensis* (Dawson numbers 10964, 10909, 10890, 8600, 10944, 8377, 10767 in US) as well as the type material of *C. clarionensis* clearly indicates that these are two different species. Dawson's material is of *C. aduncum* Nakamura, showing tetrasporangial and nodal arrangements characteristic of this species.

Ceramium aduncum also resembles *Cer-*

amium ornatum Setchell & Gardner (1930), a species also described from Isla Guadalupe. Nevertheless, in spite of the similarities in the nodal structure and in the occurrence of noninvolucrate tetrasporangia in both species, *C. ornatum* lacks the typical gland cells of *C. aduncum*. In addition, *C. ornatum* has tetrasporangia located in whorls protruding from the upper half of the nodes, which contrasts with *C. aduncum*, in which tetrasporangia are scattered adaxially throughout the node.

MATERIAL EXAMINED: *Ceramium clarionensis*, Vietnam: Cau Da, us03641 (in part *Ceramium aduncum* and other *Ceramium* spp.) leg. E. Y. Dawson. *Ceramium "clarionense"*, Mexico: Isla Guadalupe, us006818, us006819, leg. E. Y. Dawson; Baja California, us006815, leg. M. Neushul; Bahía Santa Maria, us006820 (in part "*C. clarionense*" and *C. sinicola* var. *sinicola*), leg. E. Y. Dawson; Sinaloa, us006821, us006823, us006824 (only *C. flaccidum*), us006826, leg. E. Y. Dawson; Oaxaca, us006825, leg. E. Y. Dawson; us40834, leg. A. E. Dennis. *Ceramium* sp. nov.?, Mexico: Isla Guadalupe, us1462250, leg. H. L. Mason. *Ceramium aduncum*, O'ahu Island, Ka'alāwai, m812-m836, leg. I. Meneses; Maui Island, Mā'alaea Bay, IAA14499, leg. D. P. Abbott.

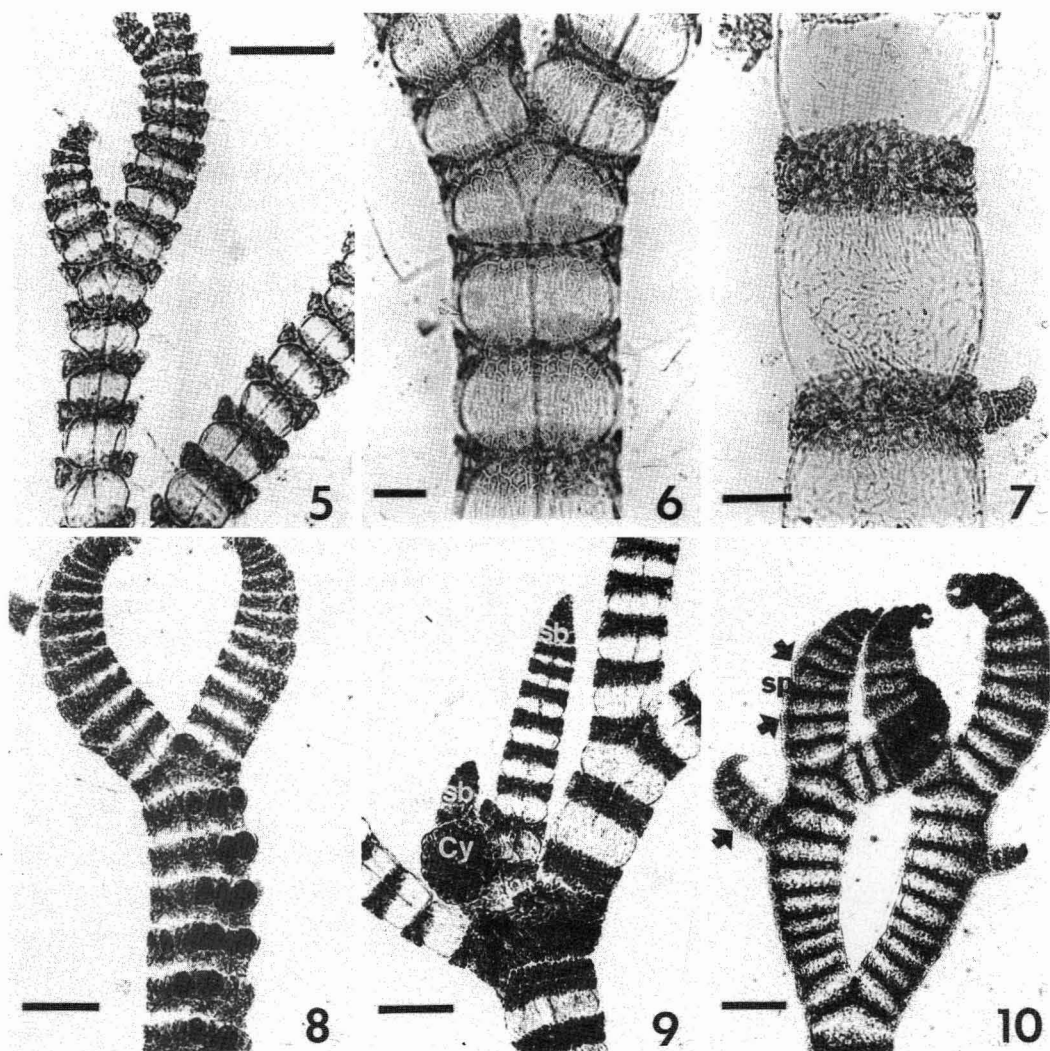
DISTRIBUTION: California (Dawson 1950, 1961). Mexico: Baja California and Nayarit (Dawson 1950, 1961, 1962); Gulf of California, Sonora, and Sinaloa (Dawson 1961, 1962). Hawaiian Islands: O'ahu (this study). Marshall Islands (Dawson 1956, 1957a). Japan (Nakamura 1950, 1965, Itono 1972). Taiwan (Formosa) (Nakamura 1950, 1965). Vietnam (Dawson 1954b).

Ceramium clarionensis Setchell & Gardner
Figures 5–10

Ceramium clarionensis Setchell & Gardner, 1930:170, pl. 7, figs. 26–27; non *C. clarionensis* sensu Dawson, 1950:134, pl. 4, fig. 29; non *C. "clarionense"* sensu Dawson, 1954b:448, fig. 55K; 1956:54; 1961:440; 1962:53, pl. 18, figs. 5–6.

Plants always epiphytic on a variety of red

algae occurring subtidally, in areas subjected to medium wave exposure. Thallus 2–9 mm long, basal portions horizontally attached to the substrate and upper portions remain free and grow upright. Branching pattern dichotomous, usually three or four dichotomies present throughout the thallus, exceptionally up to six dichotomies present; numerous adventitious branches formed, up to 12–13 per plant. Apices strongly incurved only at the very tip. Attachment by adventitious, uniseriate rhizoids either having a blunt apex or ending in small digitations. Nodes and internodes clearly distinguishable (Figure 5). Internodes slightly wider than long in upper portions where the cells are ovoid and flattened (Figure 6), becoming longer downward (Figure 7) and clearly distinguishable from nodes. A cytoplasmic strand running from cell to cell in the center of the filament is present in living as well as fixed material (Figure 6). Internodes (96)144–200 μm in diameter and 35–112 μm (sometimes up to 138 μm) long in the basal portions of the plant; 120–170 μm in diameter, 12–96(108) μm long in the upper portions of the thallus. Nodes generally not swollen, with a ratio of 1:1 in node to internode diameter, occasionally thicker; consisting of three to four cortical cell rows, six to seven rows in the most developed basal portions of the thallus, initially observed as a central row of large pericentral cells surrounded by one to two rows of cortical cells later entirely covered by cortical cells (Figure 7); nodal diameter 135–200 μm and nodal length 50–100 μm in the prostrate portion; 130–180 μm diameter, 60–90 μm long in the upright portion. Cortical cells 9–19 μm (up to 26 μm) by 9–16 μm (up to 19 μm); irregularly shaped, either angular or rounded. Tetrasporangia in the upper half of primary and adventitious branches occurring in whorls, the lower half partially embedded in the cortical band (Figure 8); tetrasporangia obovate, 35–64 by 32–51 μm in diameter surrounded by three- to four-celled involucre originating from cortical cells. Carposporangial plants irregularly branched, with the upper portion of the branches slightly swollen. Gonimoblasts subterminal (Figure 9), with up to six subtending branches



FIGURES 5–10. *Ceramium clarionensis* Setchell & Gardner. 5, Overview of branching pattern; scale = 170 μm . 6, Close-up of nodal and internodal structure with cytoplasmic strand; scale = 50 μm . 7, Close-up of fully developed nodes in lower portions of the plant; scale = 70 μm . 8, Tetrasporangial plant; scale = 140 μm . 9, Cystocarpic plant; one gonimolobe (Cy) visible among subtending branches (sb); scale = 120 μm . 10, Spermatangial plant with spermatangia (sp) on the cortex (arrows); scale = 112 μm .

frequently incurved but without forcipate apices; the main axis growing beyond the gonimoblast; two equally developed gonimolobes usually present; 21–53 by 20–41 μm in diameter. Spermatangial plants primarily dichotomous with secondary formation of adventitious branches, upper portions of branches slightly swollen. Spermatangia cov-

ering cortical cells in nodes (arrowheads in Figure 10) in the upper half of the plant.

REMARKS: This species is especially distinctive in its tetrasporangial features. Type material as well as Hawaiian plants of *C. clarionensis* show tetrasporangia initially abaxially located and eventually becoming

whorled with involucre. Tetrasporangia from the type specimen are slightly larger (65–75 μm diameter) than those from Hawaiian material.

Depending on the degree of cortical development, pericentral cells can sometimes be easily observed as a central row of large cells, which, with age, become completely indistinguishable. The formation of new layers of progressively smaller cortical cells considerably changes the appearance of the cortical band. Nevertheless, the nodal diameter and length remain fairly uniform throughout the thallus of an individual plant and show no discernible variation between different plants. In comparison with the type specimen of *C. clarionensis*, Hawaiian plants show a larger number of rows formed by smaller cortical cells per node. But internodes of Hawaiian material are slightly longer and thinner in the basal creeping portion of a plant as compared with its upright portion.

Setchell and Gardner (1930:170) described "stiff trichoblasts," 30–35 μm long, originating from the upper cells of the cortical bands. These trichoblasts were not observed in the type material nor were they detected in the Hawaiian plants. Setchell and Gardner (1930) were probably referring to structures that did not withstand the methods employed to preserve the type material. Because the degree of hair formation has been shown to vary with nutrient concentration (De Boer and Whoriskey 1983), their occurrence is probably dependent on the growing conditions of the plant; their utility for species discrimination is thus unlikely.

Ceramium clarionensis has been confused with *C. aduncum* Nakamura (Dawson 1950, 1962, Nakamura 1965:140). Although the two species are clearly distinguishable on the basis of tetrasporangial features, vegetatively the plants are very similar. In Hawai'i both species grow in the same habitats, have creeping and upright portions, and reach similar sizes in the field. The basal portions of some plants of *C. clarionensis* exhibit highly developed nodes similar to those of *C. aduncum*. In addition, some plants of *C. aduncum* may have gland cells, accentuating the similarity between the two species. Examination

of apical regions in sterile plants, however, has proved to be useful in separating specimens of the two species based on the following features: (1) flattened, transversely ovoid axial cells are always visible in the upper portions of the branches of *C. clarionensis*, whereas in *C. aduncum* axial cells are progressively covered by cortical bands; (2) the presence of gland cells in the nodes in most sterile plants of *C. aduncum* but absent in *C. clarionensis*; and (3) on the basis of their tetrasporangial features: *C. clarionensis* has slightly larger tetrasporangia that are involucre and located in whorls in the upper half of the nodes, and *C. aduncum* has mainly adaxially located tetrasporangia without involucre and distributed throughout the entire length of the nodes.

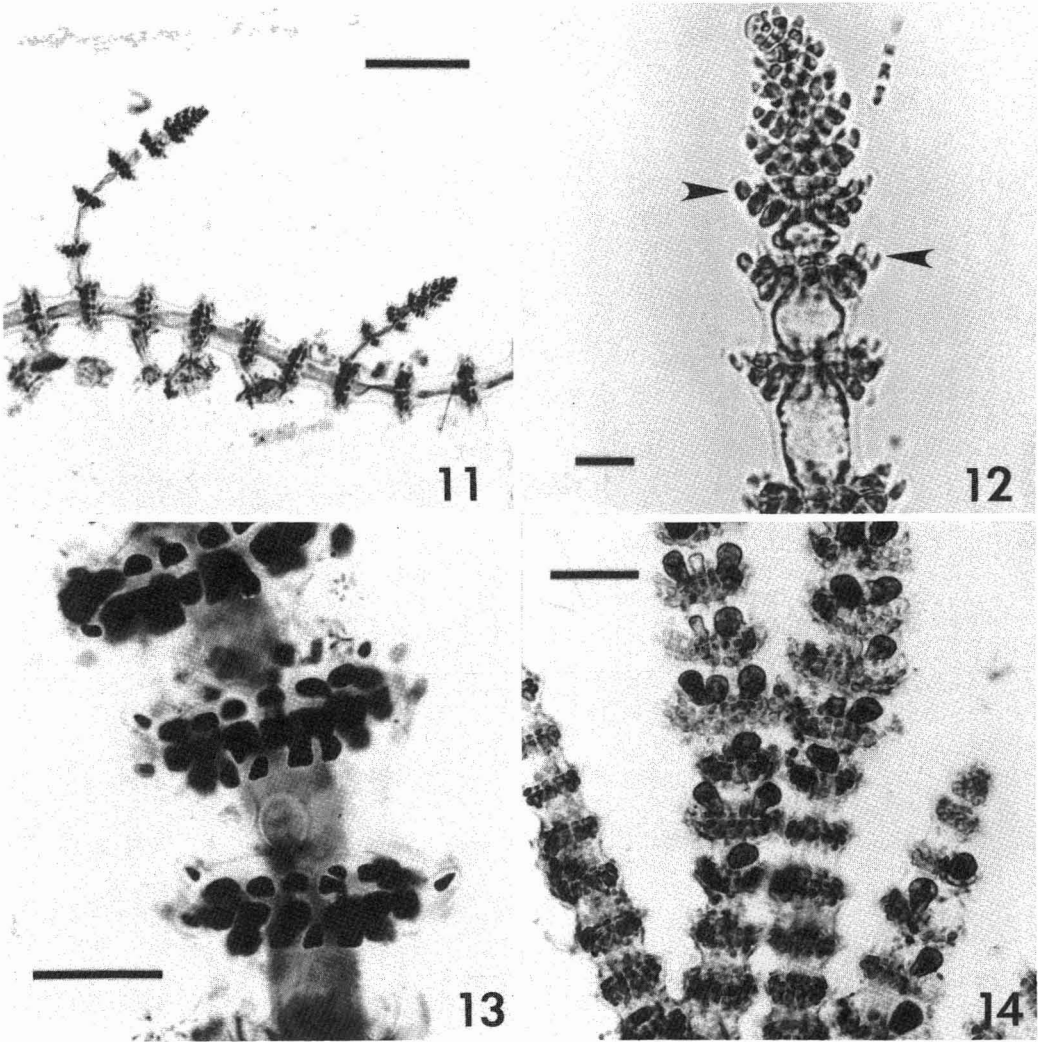
Whorled, involucre tetrasporangia are also shown by *Ceramium mazatlanense* Dawson (1950:130–132, pl. 2, figs. 14, 15). This species is apparently sympatric with *C. clarionensis* in certain areas (Dawson 1962). *Ceramium mazatlanense* differs from *C. clarionensis* in having short cortical bands (25–30 μm long) and tetrasporangia up to 35 μm in diameter, exceeding the nodal length.

MATERIAL EXAMINED: *Ceramium clarionensis* (type), Mexico: Clarión Island, CAS in UC173620, leg. H. L. Mason. *Ceramium clarionensis*, O'ahu Island, Kaloko Point, IM546, leg. I. Meneses; Hanauma Bay, IM12–IM14, IM32, leg. J. Lewis; Sans Souci beach, IM9–IM11, IM25–IM28, IM30, IM31, IAA18520, leg. J. Lewis; IM703–IM707, IM723, leg. I. Meneses; Mākaha Caverns, IAA18858, leg. L. M. Hodgson; Kahanahāiki, IAA17051, leg. W. H. Magruder. Hawai'i Island, Keāhole Point, IAA12720, leg. E. C. Haderlie.

DISTRIBUTION: Mexico: Revillagigedo Islands (Setchell and Gardner 1930). Hawaiian Islands: O'ahu (this study); Hawai'i (this study).

Ceramium cingulum Meneses, n. sp.
Figures 11–14

DIAGNOSIS: Caulis minusculus, consistens porcione postrerna causando adventicie ramuli unius lateres erectae dorsualiter et rhi-



FIGURES 11–14. *Ceramium cingulum* Meneses, n. sp. 11, Overview of a plant with prostrate and erect axes and rhizoids; scale = 750 μm . 12, Close-up of an apex with nodes showing one-celled projections (arrowheads); scale = 20 μm . 13, Nodal structure; scale = 35 μm . 14, Whorled tetrasporangia; scale = 20 μm .

zoidum ventraliter; ramuli erectae 1–2.5 mm alti. Ramification bifurca. Apices rectus aut leviter incurvi in suo extremo. Radicibus haerens per rhizoidum breves, unius cellulae fundamentis digitis et per rhizoidum longae, duae et tres cellulae extremarum simarum. Internodi 36–50 μm diametri, 36–48(156) μm largi axibus postrerni; 29–38(61) μm diametri, 48–64(90) μm largi axibus erectis. Nodus terni series lacunosae occasione data

usque seni series; cellulae pericentrales fastigati viso superficiali. Cellulae corticis externae dispositae ad effigiem vim distinguendi habens consesionis ordine ortus; duae series lacunosae acropetales, quisque cellulae formae cylindricae causando projectionem unam lacunosam (6–10 μm longae) constituta ad forsis, tertia series cortex externae basipetal, cellulae ad effigiem vim indefinita, margenes angulares, leviter protentae directione verti-

cali. Proiectiones unus lacunosae verticillibus nodum continens. Tetrasporangia a semi altitudo exibus erectis, verticillatis, meritissimi, ovatus aut obovatus, 26–42 per 22–38 μm diametri, porcio eminens involucre.

Plants epiphytic on other red algae (e.g., *Laurencia nidifica* J. Agardh, *Amansia glomerata* J. Agardh). Thallus minute, consisting of a prostrate portion with a horizontal axis adventitiously producing unilateral upright branches dorsally and rhizoids ventrally (Figure 11); upright branches ranging from 1 to 2.5 mm in height. Branching pattern dichotomous in upright axes, although branching is rare in upright as well as in prostrate axes. Apices straight or slightly curved at the very tip (Figure 12). Attachment by means of short, single-celled rhizoids with digitate bases and by long, two- to three-celled rhizoids with blunt apices. Internodes 36–50 μm in diameter, 36–48 μm (occasionally up to 156 μm) long in prostrate axes; 29–38 μm (sometimes 61 μm) in diameter, 48–64(90) μm long in upright axes. Nodes tumid (Figure 13), consisting frequently of three cell rows, occasionally up to six cell rows; pericentral cells pyramidal when observed in surface view, with the base of the pyramid oriented basipetally. Nodes 48–50(96) μm in diameter, 24–36(72) μm long in prostrate filaments, 42–55(74) μm in diameter, 19–27(32) μm long in upright axes. Cortical cells distinctively arranged according to their order of appearance; the two first rows forming acropetally, each of the cells cutting off a one-celled projection (6–16 μm long) directed outward, the third cortical cell row (Figure 13) forming basipetally after the projections are formed. Cortical cells from the two upper rows cylindrical, with long axis transverse. Cortical cells from the lower row irregularly shaped, generally with angular margins and slightly elongated vertically. One-celled projections placed in whorls around the nodes. Tetrasporangial plants frequently swollen in upper portion of upright branches. Tetrasporangia always in nodes at middle height of upright branches, in whorls (Figure 14), protruding from cortical band, ovate to obovate, 26–42 by 22–38 μm in diameter,

upper half involucre. Gametophytic plants unknown.

TYPE MATERIAL: Holotype: I. Abbott no. 18004a, a microscope slide deposited in BISH (no. 617-240) from Ka'uiki Head, Hāna, Maui Island, Hawai'i, leg. D. P. Abbott, 26 August 1976, epiphytic on *Amansia glomerata*, 1–2 m depth. Paratype: ssuc 6078 (originally IM724, IM735), specimen from Kaloko Point, O'ahu Island. Collected epiphytes on *Laurencia* spp. in semiexposed rocky intertidal.

ETYMOLOGY: The species name derives from the Latin word *cingulum*, which means girdle or belt, referring to the belt of one-cell projections present on each node.

REMARKS: *Ceramium cingulum* is characterized by clearly distinguishable prostrate and erect axes. The axes differ not only in their position, but in their origin (true versus adventitious branch formation) and dimensions. Internodal and nodal measurements of the prostrate axes are fairly consistent within the ranges given, except for a single specimen with unusually long nodes (120–156 μm long). In both prostrate and upright portions of the thallus, nodal length increases proportionally with nodal diameter within the specified ranges for the plants collected. The habit of the plant as well as the occurrence of one-celled projections located in two whorls around the nodes are two reliable vegetative features for species recognition.

Among the minute, epiphytic *Ceramium* species, there are three taxa that share the prostrate and adventitious-upright habit characteristic of this Hawaiian species. *Ceramium camouii* Dawson (1944), *C. codii* (Richards) Mazoyer (1938), and *C. serpens* Setchell & Gardner (1924) from the North Pacific and *C. codii* from the Caribbean, the Atlantic, the Mediterranean, and the Baltic Sea. None of these species, however, has the one-celled projections characteristic of the Hawaiian species. This unique vegetative feature separates the Hawaiian material from all other similar species.

Further comparisons show that the Ha-

waiian material is distinguishable from *C. camouii* in that the latter has tetrasporangia entirely embedded in the cortical bands, resulting in pronounced tumid nodes in reproductively mature asexual plants (Dawson 1944:319–320, pl. 51, figs. 2–3). *Ceramium codii* and *C. serpens* are very similar morphologically: both species have a single tetrasporangium per node (20–45 μ m in diameter), with a clearly defined involucre that partially covers the sporangium. The Hawaiian species has several tetrasporangia per node that are located in whorls and thus quite different from *C. codii* and *C. serpens*.

In *C. cingulum* the thallus structure consists of a prostrate axis with adventitiously borne upright axes that are scarcely branched, and one-celled projections are located acropetally in the nodes. These are the main characters that separate this species of *Ceramium*.

DISTRIBUTION: Known from O'ahu and Maui, Hawaiian Islands.

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